Prehistoric rock wallabies (Marsupialia, Macropodidae, Petrogale) in the far south-west of Western Australia

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Abstract

Rock wallaby remains are described from several caves in the Cape Leeuwin-Cape Naturaliste region. Measurements of cheek teeth reveal variations in size from place to place and to some extent from time to time, but there do not seem to be any accompanying differences in form. Hence the samples are regarded as conspecific, probably representing *Petrogale penicillata*. It is suggested that rock wallabies arrived in the region prior to 30 000 yr B.P. and disappeared well before historic time, the disappearance perhaps being due to replaccment of a more open vegetation by dense forest in early Holocene time.

In an appendix, there is a record of the arrival of the dog prior to the local extinction of the thylacine, and in another appendix, the presence of *Lagorchestes* in the region is confirmed.

Introduction

Rock wallaby specimens had been found in various parts of south-western Australia, including the Cape Leeuwin-Cape Naturaliste region covered in this paper, in the early years of the present century, but had not been recognized as such, and had been stored in the Western Australian Museum collection with other macropods of similar size, notably *Macropus irma* and *Setonix brachyurus*. The earliest published reference to them in the Cape Leeuwin-Cape Naturaliste region appears to be that of Lundelius (1960) reporting a discovery made in 1955 in what is now called Devil's Lair. Even after this discovery, *Petrogale* was still confused with other taxa in the Museum collection. Examples are given below. My attention was first drawn to this confusion in 1965, in connection with a large collection of very juvenile *Petrogale* specimens made by D. L. Cook in 1958 in Deepdene Cave.

The present paper attempts to resolve this confusion and to review the occurrence of rock wallaby remains in a region from which they were conspicuously absent in historic time (Calaby 1971), but a notable part of the macropod fauna in prehistoric time (Baynes *et al.* 1976). I have also taken the opportunity to review some intrinsically interesting deposits which happen to include *Petrogale*, and some samples of *Petrogale* which, though restricted in character, are more extensive than those likely to be available to neontologists, and which represent a range in time as well as in space.

The report covers all *Petrogale* specimens from the Cape Leeuwin-Cape Naturaliste region in the Western Australian Museum collection at the time of writing (January 1978). It is not practicable to list their catalogue numbers, but a copy of raw data on specimens measured, including their catalogue numbers, has been lodged in the Museum library, and particular specimens are cited by number in context.

The localities from which *Petrogale* specimens have been derived are described first, beginning with the most southerly (The Labyrinth) and proceeding to the most northerly (Yallingup Cave), about 70 km away. Cave numbers are those listed by Bridge (1972, 1973) and Bridge and Shoosmith (1975). Many of the sites are mapped by Lowry (1967) in describing the general geology of the region. The locality descriptions are followed by descriptions of the samples, and these in turn by some discussion of their significance.

The present day vegetation of the region is described by Smith (1973), but there may be considerable differences between the vegetation in historic time, and that of the prehistoric period during which *Petrogale* flourished (Balme et. al. 1978, Churchill 1968).

Localities

The Labyrinth (AU16).—The general form of this aptly named cave, about equidistant from the townships of Augusta and Karridale, near Cape Hamelin, is described by Lowry and Bain (1964).

Remains of extinct marsupials were found by D. C. and J. W. J. Lowry in a passage now known as "Wombat Warren" extending north east from the chimney-like entrance. I visited the site with G. W. Kendrick and J. W. J. Lowry in 1969, collected further specimens, and made a cursory examination of the deposit. A steeply sloping talus cone descends into "Wombat Warren" from what appears to be an old entrance, now choked with sediment. Some specimens were found in or on this slope, but others were recovered from a poorly to well lithified red sandy deposit containing lumps of stalactite, ferruginous nodules, and charcoal as well as bone, suggesting it may be a lithified portion of an original talus cone below the postulated old entrance. This lithified deposit formed a ledge adhering to and projecting from the steeply sloping roof or wall of the chamber.

A short note on material recovered was published (Merrilees 1969), but this did not include *Petrogale*. However, portion of the dentary of an adult macropod (specimen 69.4.2) mentioned in this report appears to represent *Petrogale*, and another juvenile *Petrogale* dentary (66.1.3) was found in 1965 near the cave entrance by B. G. Muir.

No estimate of age is available for the Labyrinth specimens, but 69.4.2 was associated with *Sthenurus* and other extinct taxa in the lithified ledge. Specimen 66.1.3 has only slightly lithified matrix adhering to it (unlike 69.4.2), but the bone has a somewhat chalky appearance which often seems to indicate considerable age under south-western cave conditions.

Deepdene Cave (AU1).—D. L. Cook collected *Petrogale* and other specimens from the site in Deepdene Cave about to be described and presented them to the Western Australian Museum in 1958. He showed the site to P. Cook, who drew the attention of P. Henley to it, resulting in an excavation which produced a large *Petrogale* sample from a small volume of deposit. This excavation was made by P. Henley and D. C. and J. W. J. Lowry and others in 1968, and described by D. C. and J. W. J. Lowry (1968). A radiocarbon date of 19 400 ± 1 200 yr B.P. (GaK—2417, Kigoshi, Suzuki and Fukatsu 1973) was determined on the collagen of bone (mainly of juvenile *Petrogale*) from the lower half of the excavation. The cave is described briefly by Caffyn (1973).

The Lowry and Henley collection was presented to the Museum, and on analysis turned out to contain an overwhelming majority of fragments of very juvenile rock wallabies. For example in the lower half of the sample, there were 46 left upper milk molars of *Petrogale*, and hence at least 46 juvenile animals had contributed to the sample. There were probably no more than 2 adults of *Petrogale*, as judged on right first upper incisors with fully formed roots (there was only one permanent premolar with fully formed roots, the most certain indication of the presence of an adult). Minimum numbers of individuals of other taxa were as follows: murids 3, *Setonix* 2, *Bettongia penicillata* 1, *Potorous* 4, *Pseudocheirus* 2, *Trichosurus* 3 and *Isoodon* 3; some of these were adult, some juvenile. Two tooth fragments in the deposit conceivably could represent *Sarcophilus*, but this is uncertain.

The highly selected character of the sample was noted while the excavation was in progress (Lowry and Lowry 1968), and the excavators put forward three alternative suggestions as to its origin. The first was that the place might have served as the lair of some carnivore such as *Sarcophilus*. The second was that it might have been a human midden, and the third was that animals might have drowned while drinking at a pool in which the deposit was accumulating.

To these suggestions may be added two others, that the pool did indeed serve as the lair or feeding place of a predator, but this was either a large owl or a large snake. In favour of the owl suggestion is the concentration of bone in one place, provided with ready-made perches and a platform on which prey could be deposited before being eaten. Against, perhaps, is the highly selected nature of the prey, and this favours the snake suggestion.

Boids no larger than existing species might be expected to take young rock wallabies, *Setonix*, *Trichosurus* and possibly feeble or moribund individuals of even larger species, and there is a possibility that a boid very much larger than any of the existing Australian species was involved. Very large snake vertebrae are known from Mammoth Cave (Merrilees 1968) about 22 km north of Deepdene Cave, and from Koala Cave, near Perth (Archer 1973). These have been examined by Dr M. J. Smith, University of Adelaide, who believes them to be conspecific with *Wonambi naracoortensis* (pers. comm.). *Wonambi* may have reached a length of 5 m (Smith 1976) and the size of its vertebrae indicates a girth several times that of the living Australian pythons.

I have not examined the site, but estimate from notes and diagrams supplied by the excavators that rather less than 10% of the deposit has been collected. A minimum number of 252 individual animals is represented, estimated by methods described by Baynes *et al.* (1976) as amended by Balme *et al.* (1978). Assuming that in this relatively large sample from a very circumscribed deposit the conventional "minimum number of individuals" approximates the actual number, then more than 2 500 individuals were taken by the predator concerned. If this was a large animal like *Wonambi*, it might have collected 1 prey animal every few days for part of each year, in which case some 20 years accumulation is indicated. The whole deposit might be attributable to one such animal.

Strongs Cave (WI 63).—This is a very long tunnel-like cave traversed by a stream for its full length. A description and maps have been given by Williamson *et al.* (1977). It has a chimney-like entrance leading to a talus cone which has buried the stream, so that the water takes a concealed (but apparently very little impeded) course through the base. From the point where it re-emerges for some 30 m downstream, many of the small depressions in the stream bed contained isolated teeth of mammals, some of extinct taxa like *Sthenurus* (Cook 1963), among other "pebbles". Extensive collections of these isolated teeth were made and presented to the Museum, including many of *Petrogale* e.g. the four molar enamel caps now included under catalogue entry 73.11.53. But these were not at first recognized as *Petrogale*, and in 73.11.53, for example, were labelled merely as "macropods".

The presence of the extinct taxa led to some detailed study of the cave by myself and others, and some systematic excavation was undertaken in what appeared to be a remnant of the ultimate source of the stream bed specimens. This was called "left ledge" in field notes, because it was on the left bank of the stream in the entrance chamber, and had a gently sloping surface standing several metres above the steeply sloping surface of the talus cone burying the stream. "Left ledge" and its opposite number "right ledge" appear to be the remnants of an older talus cone which has been undermined by the stream and let down in its central portion. This central portion may have received accretions of sediment, including teeth and bones, more recently than "left ledge", and some of this younger material may have found its way into the stream bed. Thus the teeth collected in the stream bed might be of various ages.

The excavation on "left ledge" reached what appeared to be an unfossiliferous basement of tumbled limestone blocks and fragments at very shallow depth. Nevertheless, it proved to contain extinct taxa (e.g. specimen 65.9.28, *Sthenurus brownei*) and *Petrogale* (e.g. 65.9.11), suggesting some considerable age for at least some of the *Petrogale* specimens recovered. However, no radiometric dates are available for Strongs Cave. The older Strongs Cave fauna (ignoring extant taxa known only from surface litter or from the stream bed) is listed by Merrilees (1968).

Although man, *Sarcophilus* and other predatory species are recorded from Strongs Cave, there is no other reason to postulate that it served as a predator's feeding place. On the contrary, the nature of the cave entrance suggests a "pit trap" effect, accounting for the presence of the predatory as well as the non-predatory species.

Devil's Lair (WI 61).—There are many references to and descriptions of Devil's Lair, four of which give analyses of mammal remains including *Petrogale*. These are by Lundelius (1960), Dortch and Merrilees (1972), Baynes *et al.* (1976) and—most significant for present purposes—Balme *et al.* (1978). The last paper re-examines suggestions made previously and attributes mammal (and other) remains in the deposit initially to owls (up to about 30 000 yr. B.P.) and then to human beings (sporadically), *Sarcophilus* (perhaps more consistently, between short periods of human occupation) and owls (probably diminishingly after about 30 000 yr. B.P.).

Petrogale is first represented in the Devil's Lair deposit in what Balme *et al.* (1978) designate Layer 29 and estimate to be a little less than 30 000 years old. But its representation from this layer up to Layer 11 is very sparse, and includes some doubtful specimens such as upper molar 77.4.652 which is so worn as to obscure its *Petrogale*-like characteristics. However, there are undoubted specimens in these older layers. *Petrogale* begins to be more abundant in Layer 10, and from Layers 6 to D (i.e. from somewhat later than 19 000 yr. B.P. up to the not precisely known but approximately mid Holocene time of formation of Layer D), it is fairly abundant.

Flowstone layer D was partly buried by a black humic redistributed forest floor soil apparently about 300 years ago when the cave was re-opened in a new place. There was considerable disturbance of this uppermost black Layer A by the first excavators, and it is often difficult to decide whether a given segment has or has not been disturbed. *Petrogale* is recorded from Layer A, but I have re-examined the specimens concerned, and consider it possible that they are secondarily derived from excavated material. In view of the absence of historical records of *Petrogale* and of its absence from two dated deposits including late Holocene material—Skull Cave (Porter in press) and Deepdene Cliffs (Archer and Baynes 1973, a site near to but not identical with Deepdene Cave)—I reject the Layer A record in Devil's Lair. Thus I infer that *Petrogale* vanished from the Devil's Lair district, and perhaps from the Cape Leeuwin-Cape Naturaliste region, at some mid Holocene time not at present known more precisely, but subsequent to the formation of Layer D in Devil's Lair. The relevant specimens are 73.10.61-63, 73.10.370-372, 77.6.358 (reported Layer A) and 73.10.399-402 (Layer D).

It is possible that the first appearance of *Petrogale* in the Devil's Lair deposit approximately marks the time of its arrival in the region, i.e. rather less than 30 000 years ago. This is consistent with the record, first of sparseness and then of abundance, presumably as colonies became well established or the environmental trends which led to the immigration in the first place continued, or perhaps intensified.

However, there is a proviso. The lowest parts of the Devil's Lair deposit contain specimens some of which like *Sthenurus*, cannot be regarded as owl prey, which apparently pre-date occupation of the cave by man or *Sarcophilus*, and many of which are more or less completely coated with a layer of cemented sand grains, and so present a characteristic appearance. Such specimens are regarded by Balme *et al.* (1978) as possibly secondarily derived ("re-worked") from an older deposit which they postulate as occupying a position in or near the old entrance. The existence of such a deposit is not proven, and if it exists, its extent, nature and content are known only from the small range of specimens which have become re-worked into the deposit sampled by excavation. Conceivably it could contain *Petrogale*. Indeed *Petrogale* is known to be associated with extinct taxa in The Labyrinth and Strongs Cave, and these associations may well be older than 30 000 yr. B.P. Thus the Devil's Lair indication of an arrival of *Petrogale* about 30 000 years ago and a local extinction about, say, 5 000 years ago can only be accepted tentatively.

Giants Cave (WI 21 and 22).—A single specimen, collected by P. J. Bridge in 1962, represents the *Petrogale* record for this cave. It is the horizontal ramus of a juvenile right dentary (65.12.51) which was partly encrusted with a granular matrix when found, suggesting it was not deposited very recently, but otherwise with no indication of its geological age.

Giants Cave is not notable for any abundance of mammal remains, but it has yielded *Petrogale* and *Thylacinus* (67.9.1) among locally extinct taxa. P. J. Bridge has collected *Macropus fuliginosus* post-cranial material (65.12.45) of chalky appearance cemented into a granular matrix, and I have collected fragments of an unidentified large macropod, also of chalky appearance, thickly coated with dense flowstone (66.7.3). It is possible that these specimens are of some considerable age.

The cave consists essentially of a large tunnel opening at one end from a large doline with steeply sloping but not vertical walls, and by way of a talus slope from a small doline at the other end. It would not appear to have acted as a pit trap, so presumably the bones in it were taken there by predators, or represent animals which died in the cave.

Museum Cave (WI 31).—A skull fragment labelled 12018 and several other fragments (including a right maxillary fragment) collectively recatalogued as 77.10.3 (originally stored with *Setonix* specimens) and a left maxillary and one other fragment catalogued as 77.10.1 (originally with *Macropus irma* specimens) appear to be parts of the same skull. If so, they would be part of a collection made in Museum Cave by L. Glauert (according to catalogue data with 12018 which are not in the collector's handwriting) and hence would have been collected in 1912, according to a newspaper article quoted by Mahoney and Ride (1975 p. 195).

Despite this confusion, there is no reason to doubt the authenticity of the locality record, for an old and corroded label with the *Macropus irma* specimens mentioned above (66.9.63-70) carries a pencilled inscription which, though partly obscured, can hardly be other than "Museum Cave"; it appears to be in the collector's handwriting.

There is a record by Glauert (1948), presumably the basis of one by Bridge and Shoosmith (1975), of *Thylacinus* from Museum Cave, but I can find no specimen to substantiate this record. Otherwise, the small collection of bone from the cave includes only extant species. The *Petrogale* skull fragments are fragile and partly encrusted, so that some considerable age may be postulated.

A description of Museum Cave by Caffyn (1973) suggests to me that it may have acted as a pit trap for mammals.

Yallingup Cave (YA 1).—This cave is in the north of the region, and although it has a long history as a tourist attraction and there are many published references to it (Bridge 1972), there appears to be no comprehensive description of it as yet. However, one by Williamson, Loveday, Loveday and Bell is in preparation.

My attention was drawn to it by the finding of a thylacine humerus and later a dentary (63.3.2, 63.3.42) during tourist development in 1963. I made a brief examination of this "thylacine locality" after this discovery.

Later in 1963, as part of a tourist publicity campaign, D. Williams took up residence in the cave for several weeks. She made some shallow excavations in the cave floor in consultation with me, we corresponded, and I visited the cave again at an intermediate stage of these excavations. Although the work of an amateur, unused to interpreting and reporting excavations, they were made with care and attention to detail, and not under pressure of time.

Taxa extant in the district in historic time (including *Canis*) were recovered from several shallow excavations, but at the "thylacine locality" a deeper excavation was made, reaching what appeared to be a basal layer of jumbled fragments of limestone after traversing several distinct layers. The surface sloped quite steeply and the various layers sloped in consonance with it. The uppermost layer, containing the thylacine, was a well bedded sand, up to about 40 cm thick; apart from *Thylacinus*, mammals represented were of taxa still extant. This sand rested on a thin layer called "1st dripstone" in field notes and correspondence, meaning either a thin layer of sand rendered coherent by calcareous cement, or a thin crystalline flowstone. Below this was a slightly lithified, rubbly layer containing bones, resting in turn on a "2nd dripstone". The rubbly layer varied in thickness from about 60 cm to about 110 cm. Below the "2nd dripstone" was another slightly lithified, rubbly layer about 45 cm thick, resting on the basal layer of rocks. Excavation was discontinued at this rocky basal bed because excavated material began to be lost in open crevices between the rocks.

No specimens were recorded from the "dripstones", but abundant mammal and some other remains were found in both layers below the respective dripstones. These layers consisted predominantly of sand, but with numerous limestone clasts, the whole slightly lithified. They were excavated in arbitrary 7½ cm, 15 cm or 30 cm "spits" because of their substantial thickness.

Petrogale (63.7.184-189, 63.7.203, 63.8.9, 63.8.12-15, 63.8.19-22, 76.6.39, 76.2.99-100, 76.2.107-111, 77.10.2 and 78.1.66) is a conspicuous component of the fauna recorded below "2nd dripstone". Other taxa represented below "2nd dripstone" included the murids *Notomys, Pseudomys albocinereus* (neither known from the region in historic time) and *Hydromys* (indicating the presence of free water), together with an unidentified snake of medium size, *Bettongia lesueur* (not known in the district in historic time) and various mammal species still extant in the region. Snake vertebrae (76.2.112-114) occur in all three of the arbitrary "spits" excavated below "2nd dripstone"; it is possible that these vertebrae derive from the same animal, emphasizing the arbitrary character of the divisions. *Canis* appeared just below "1st dripstone" (see Appendix 1).

In another part of the same chamber in which D. Williams made her excavations, G. Pick also made excavations in an attempt to find extensions of the chamber. Excavated material was systematically sieved, bone was recovered, and its depth recorded. Towards the bottom of the tunnel so excavated, about 4 m below the cave floor, a single *Petrogale* tooth (77.8.51) was recovered. It is an upper permanent premolar, probably unerupted, though it appears to have undergone some root development. The enamel is somewhat mottled, there is adhering matrix, and this appearance and the depth of burial suggests that its age is considerable.

The Petrogale samples

Measurements

All the available material consists of broken bones. I have studied only tooth-bearing specimens or isolated teeth, have measured only cheek teeth, and have concentrated statistical attention on the anterior cheek teeth ($P^3{}_3$, $dP^4{}_4$, $P^4{}_4$ and $M^1{}_1$ on the Thomas 1887 notation, or deciduous premolars, milk molars, permanent premolars and first molars respectively). Some data on posterior molars are included.

All measurements were made by me in November and December 1977 by applying the sharp points of dial vernier calipers over the tooth concerned in a plane judged to be perpendicular to the palate. There is some subjectivity in this, and although results were recorded as though correct to 0.1 mm, this probably exaggerates their reproducibility; however, the practical alternative of correcting to 1.0 mm would have underestimated their reproducibility. "Length" was measured in the plane of occlusal contact of the tooth concerned with those before and behind (or a projection of this plane in the case of the first and last teeth in a row). "Width" was a maximal record, for premolars, usually about central in a lower deciduous premolar, and posterior in a milk molar, a permanent premolar or an upper deciduous premolar. For a molar, "width" was used statistically only when the crown of the tooth concerned rose above the alveolar margin, as records for molars excavated from their crypts suggested that this measurement was otherwise unreliable. Anterior widths are recorded for molars, with posterior width added for $M^4{}_4$, in which differences between anterior and posterior widths may be substantial.

The Deepdene Cave sample was considered in three divisions for statistical purposes, the upper half and lower half of the Lowry and Henley excavation separately, plus a third division ("age uncertain") made up of unlocalized specimens from this excavation and from the earlier Cook excavation.

In recording measurements on Devil's Lair specimens, three divisions, or grades of insight into relative ages, were recognized. The material covered by Balme *et al.* (1978), with numerous stratigraphic divisions and a series of radiocarbon dates, was regarded as most reliably dated. Next came material reported by Baynes *et al.* (1976) and Dortch and Merrilees (1972), based on thick stratigraphic divisions, and only tentative correlation between separate trenches. "Young", "intermediate" and "old" specimens were separated in this division. "Young" means approximately early Holocene, and covers specimens recovered from Trench A1 above the rubbly layer at 151-154 cm illustrated in Figure 2 of Dortch and Merrilees (1972), from Trench 6 above "brownish earthy layer" (Fig. 3 of Dortch and Merrilees 1973) and from Trenches 2 and 5 above "first orange brown earthy layer" (Figs. 4 and 5—left of Dortch and Merrilees 1973). "Intermediate" means late Pleistocene, (post-glacial-maximum) approximately, covering lower levels in Trench A1, "brownish earthy layer" in Trench 6, and "first orange brown earthy layer" in Trenches 2 and 5. "Old" means late Pleistocene, (pre-glacial-maximum) approximately and covers the lowest layers in Trench 5 and as far down as Layer 28 in Trench 2, but not including the contents of Pit 2 (see Fig. 4 of Balme *et al.* 1978). There were in fact very few specimens in the "old" group. Finally, an "age uncertain" division was recognized in Devil's Lair, made up of specimens collected prior to the systematic series of excavations which began in 1970 plus those dislodged during extensive section cleaning or disturbed in other ways during the systematic excavations. For most statistical purposes, the accurately localized Balme *et al.* material was apportioned as "young", "intermediate" or "old". "Young" was taken to mean Hearth 2 and upward (excepting material allegedly from Layer A but here considered to be disturbed and hence in the "age uncertain" division). "Intermediate" meant Layers 8 upward to M inclusive, with the contents of Pit 2. "Old" meant Layers 9 and downward.

The Yallingup Cave sample, although small, has been kept separate for statistical purposes, mainly because the northerly position of this cave might imply substantial climatic differences between it and, say, Deepdene Cave. The small samples from the other caves have been combined for statistical purposes.

Two small samples of modern *Petrogale* from regions as close to the Cape Leeuwin-Cape Naturaliste region as were available, are also treated statistically. These are from Mondrain, Wilson and Combe Islands in the Recherche Archipelago, treated as a single sample ("Recherche"), and from a restricted area near Qualrading. Single specimens from other localities, mostly modern, were also measured; not only of *Petrogale*, but also of other macropods (Tables 9, 11).

In the case of the posterior molars ($M^2{}_2$, $M^3{}_3$ and $M^4{}_4$) the Deepdene Cave and Devil's Lair samples have been treated as one, and arithmetic means for the whole fossil sample treated as one are also shown for all teeth measured, in Table 9.

In each sample, measurements were made of teeth of one side only, nearly always the left. Thus each upper and each lower measurement of a given tooth represents a distinct individual, though that individual might be represented also by other teeth. Teeth so worn as to give a distorted impression of their original size were measured, but not included in statistical operations. Isolated molar teeth, or sometimes even one or two teeth in a maxillary or dentary fragment, also were not included in the statistics unless their position in the tooth row could be established with confidence.

Tables 1-11 summarize this metrical information. In them "N" means number of individuals in the sample, "O.R." the observed range in size, "$\bar{X}$" the arithmetic mean, "s" the standard deviation, "V" the coefficient of variation, "t" the Student's-t statistic for comparison of means. In these statistics and in the estimation of significance based on them I follow Simpson *et al.* (1960).

Some characteristics of Petrogale *teeth, and differentiation from other macropods*

Rock wallabies have teeth (Figs. 1-3) of typically macropodine form, as described and illustrated, for example, by Bartholomai (1975). But unlike *Macropus fuliginosus,* they retain functional premolars throughout life. (An exceptional modern specimen is M6208, which has lost its right upper permanent premolar, though all three other permanent premolars are still present and do not show exceptional wear). Molar progression often results in compression of the first molar against the permanent premolar, with consequent distortion of its shape and loss of its substance (e.g. 63.7.99c), or even in rare cases (e.g. M4094), total loss. M^2_2 also may be reduced in length (e.g. 77.5.558) or even width (e.g. 63.7.95c) by wear occasionally.

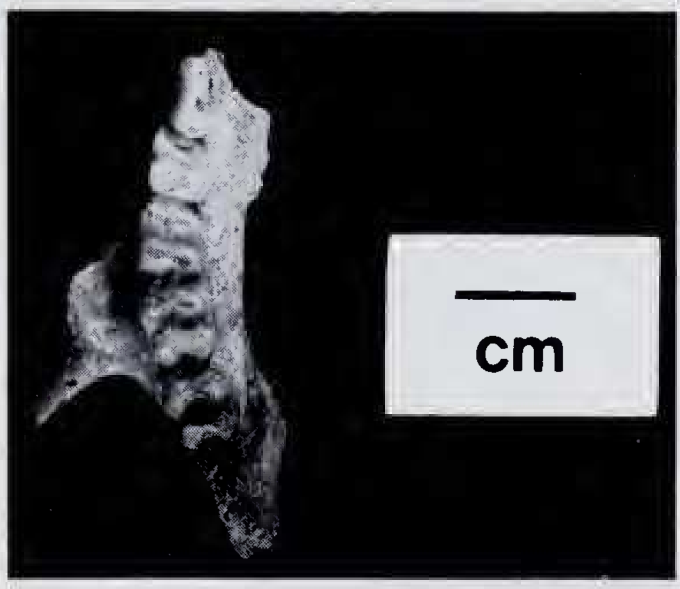

Figure 1.—*Petrogale.* Occlusal view of 63.8.15 from Yallingup Cave, showing adult maxillary cheek teeth (P^4, M^{1-4}).

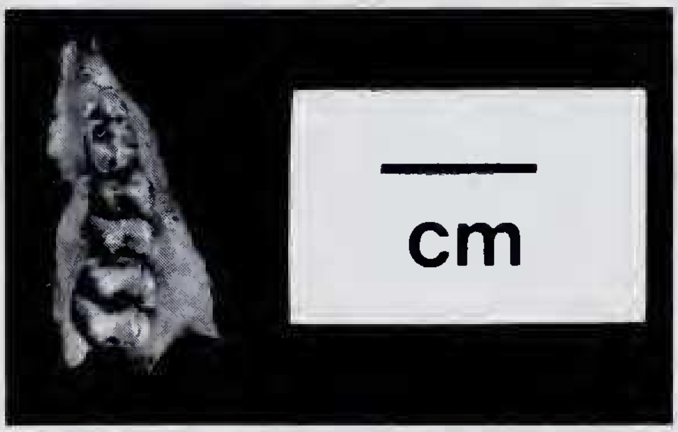

Figure 2.—*Petrogale.* Occlusal view of 77.5.473 from Devil's Lair, in which P^3 resembles P^3 of *Setonix.* Other teeth shown are dP^4 and M^1.

Figure 3.—Right upper first incisors of very young rock wallabies from Deepdene Cave, lingual aspect. Tooth on right (part of 76.2.58) has accessory cuspule well developed, that on left (part of 76.2.59) has subdued buttress not terminating in a discrete cuspule.

The molars are slow to erupt (as shown indirectly by the N columns of Tables 1-6), and the fourth molar appears never to erupt before the permanent premolar, by which time the first molar may be extremely worn (e.g. 77.5.638). In this respect, *Petrogale* differs markedly from *Setonix,* and is perhaps more extreme than the other two macropods (*Macropus irma* and *M. eugenii*) with which it has been confused in the south-west. Lower molars apparently erupt before the corresponding uppers (e.g. M4426).

Like many macropodines, but unlike the south-western potoroines, *Petrogale* shows progressive increase in molar size from front to rear (Table 9), so that the fourth molars are much larger than the first (Tables 4 and 6). In this respect, *Petrogale* differs from *Macropus irma,* in which the gradient in molar size is generally less, and indeed in which the fourth molars may be smaller than the third (Table 9).

The anterior portions of the molars in *Petrogale* are generally larger than the posterior, and this is very noticeable (and is statistically significant—Tables 6, 7) in the fourth molars, to the extent that an isolated molar tooth, even if its size falls in the overlap in range between third and fourth molars (Tables 5, 6), may be identifiable as a fourth rather than a third by this posterior reduction.

A given molar of *Petrogale* is generally smaller than the corresponding one in *Macropus irma* but larger than in *M. eugenii* and *Setonix* (Table 9) and if its position in the tooth row is known, this size difference is apparent to the naked eye, and confusion is unlikely. However, with molars of uncertain position, in which size is a poor guide to identity, there are some distinctions in form discussed by Merrilees and Porter (in press). For example, the buccal portion of the anterior shelf in $M_{3,4}$ is more completely enclosed by a low marginal rim in *Petrogale* than in *Macropus irma*, while the anterior shelf as a whole is relatively narrower and more "nose-like" in all lower molars of *M. eugenii* than in *Petrogale*. In $M^{2,3,4}$ in *Petrogale*, unlike *M. irma* or *M. eugenii*, the median valley is closed by a longitudinal low crest or partial cingulum on its lingual side. The molars of *Setonix* are distinctive and small, and hence not likely to be confused with those of *Petrogale*.

On the other hand, both deciduous and permanent premolars are large relative to the molars in *Setonix* (Table 9), and are comparable in size and in shape with those of *Petrogale*, so that the two taxa are easily confused, whereas these premolars are small relative to the molars in *M. irma* and *M. eugenii* and differ markedly in shape from those of *Petrogale*. But care is needed to distinguish an isolated upper permanent premolar of *M. eugenii* from an isolated upper deciduous premolar of *Petrogale*. There is also some possibility of confusion in milk molars in that the upper milk molar in *M. irma*, though larger than that of *Petrogale*, is not unlike it in shape.

Some criteria for distinguishing premolars and milk molars of *Petrogale* from other taxa with which confusion is possible are as follows:—

1. Deciduous premolars. In *Petrogale*, P^3 is likely to be marginally longer and narrower than in *Setonix* (Table 9) giving a visual impression of narrowness in direct comparisons. In both taxa there is a central longitudinal depression, which is subdivided by more numerous and better developed (but still minor) transverse crests in *Setonix*. The most anterior and most posterior of the small compartments so formed in this depression are narrower and more obviously inclined to the longitudinal axis of the tooth in *Petrogale*. In *M. eugenii*, P^4 is usually shorter and narrower than P^3 in *Petrogale* (Table 9), and the lingual low longitudinal crest which in P^3 of *Petrogale* (and *Setonix*) helps to define a central depression is confined to the rear part of the tooth in P^4 of *M. eugenii*, so that there is no anterior compartment. In *Setonix*, P_3 is generally marginally shorter and wider than in *Petrogale*, giving a visual impression of its being a stouter tooth, which impression is strengthened by its having its maximum width anterior, whereas P_3 in *Petrogale* is quite narrow anteriorly.

2. Milk molars. As in most macropodines, the milk molars in *Petrogale* are generally molariform in shape, and yet easily recognizable as milk molars (dP^4_4) by their anterior constriction and distinctive anterior shelves. The most likely confusion would appear to be between *Petrogale* and *M. irma* in dP^4; however the latter is substantially larger (Table 9). Further, in dP^4 in *Petrogale*, the buccal corner of the anterior shelf is more angular in plan, the fore- and mid-links more pronounced, and the median valley more definitely truncated buccally by fusion of crests ascending from the paracone and metacone, than in *M. irma*.

3. Permanent premolars. In *Setonix*, P^4 appears to be rather variable in size and shape, but is often somewhat longer, lower crowned and more uniform in width than that of *Petrogale*, which is considerably wider posteriorly than anteriorly (Fig. 1). Likewise, P_4 in *Setonix* tends to be longer and wider than in *Petrogale*, but there is a good deal of overlap (e.g. in Table 9) and in both taxa, P_4 is blade-like, with a longitudinal crest which is inflected lingually at the rear. In relatively unworn teeth, this crest is seen to be slightly serrated, because of a longitudinal succession of cusps. The most anterior of these tends to be the most prominent in *Petrogale*, whereas in *Setonix* the two most anterior are more nearly equal in prominence. There is a longitudinal cingulum, not very pronounced, but sometimes present on both buccal and lingual faces of P_4 in *Petrogale*, whereas it is usually very inconspicuous or missing entirely from the buccal side in *Setonix*. In both taxa, a crest descends from the most anterior cusp to form the front of the tooth, and in *Setonix* this front crest projects further forward at the enamel margin than in *Petrogale*, in which the descent is more nearly vertical. But none of these differences is marked, and in practice it is sometimes very difficult to decide on the identity of an isolated P_4. Fortunately, where any of the more posterior teeth is present, the distinction between *Petrogale* and *Setonix* is clear.

Lower incisors in *Petrogale* and *Setonix* are similar in shape and size, and retain a leaf-like appearance for a larger proportion of the animal's life than in *M. irma* or *M. eugenii*. They are generally slightly narrower (laterally) where they emerge from the bone in *Petrogale* than in *Setonix*, and are more incumbent than in *Setonix*, *M. irma* or *M. eugenii*.

Upper incisors in all four taxa are similar in general form, i.e. the first is a slightly curved blade, the second of approximately equidimensional section, and the third lobate. Those of *M. irma* are noticeably larger than of *Petrogale*, *Setonix* or *M. eugenii*. In the last three taxa, size differences are a poor guide to identity, and are often obscured by wear differences. A small peg-like cuspule standing out from the lingual face of I^1, originating about half way down in an unworn tooth, nearer to the posterior border, is very characteristic of *Petrogale* where present (Fig. 3). However, as discussed under "variability", this cuspule is not always present, and a somewhat similar cuspule occasionally appears on I^1 in other taxa (e.g. 77.6.142 or M1760, *M. irma*). Detailed criteria for distinguishing upper incisors are given by Merrilees and Porter (in press).

Variability in Petrogale *teeth*

The coefficients of variation in Tables 1-6 show not only that populations in a given place and time are fairly or very uniform in tooth dimensions (note Tables 2, 4 especially), but also that they are still uniform when time is disregarded (Deepdene Cave and Devil's Lair entries in Tables 5, 6). However, somewhat greater variability in deciduous and (more notably) permanent premolars, and in widths rather than lengths, is recorded in Tables 1 and 3.

Time can be taken into account most clearly in the succession summarized in Table 10. So far as statistical tests on the small stratigraphic samples of Table 10 have meaning, it may be noted that the difference between the means of length of P^3 in Layer Q and Layers 4, 5, 6 combined is significant (5% level, $t = 2.60$, degrees of freedom $= 10$), as also for length of P_3 in Layer O and Layers Y and Z combined ($t = 3.80$, degrees of freedom $= 8$). These, and some other differences which are not statistically significant (e.g. length of dP^4 in Layer O compared with Layers 10 d and e) suggest there was some tendency for tooth size to increase in the *Petrogale* population around Devil's Lair as time went on. But other differences (e.g. between length of M_1 in Layer O compared with Layer 6—not statistically significant) are opposite in trend, and none of the apparent trends is very marked.

There are some variations in shape as well as size among *Petrogale* premolars, and many of these variants resemble *Setonix* even more closely than modal specimens do.

A fairly common variant of P^3 in *Petrogale* is the development of a "pocket" in the enamel of the buccal face towards the front of the tooth (e.g. 77.5.473 Fig. 2). Sometimes this is accompanied by an enamel fold towards the back of the tooth (e.g. 75.4.243). Particularly in the latter case, the tooth comes to resemble a P^3 of *Setonix* quite closely. In fact, 75.4.243, an isolated tooth, was initially identified as *Setonix,* and even after re-examination and ascription to *Petrogale,* remains a somewhat doubtful case.

Partial development of a buccal cingulum, as these structures in P^3 perhaps could be described, may occur also in P_3. For example, in 73.11.807, the middle third of the buccal face of the tooth carries a distinct cingulum, developed into a deep pocket in the enamel of the posterior third. Another variant of P_3 is extreme lingual inflexion of the posterior part of the crest forming the blade-like occlusal part of the tooth. In 77.6.483, this posterior portion of the crest is transverse, approximately perpendicular to the (major) anterior portion of the crest, which is nearly parallel to the longitudinal axis of the tooth.

Variants of the modal milk molar form appear not to be common, a matter of some importance in the discussion (in Appendix 2) of 70.12.1132. However, in 77.12.1, the forelink is interrupted, the more anterior portion crossing the anterior shelf obliquely, whereas usually the forelink rises continuously from the anterior shelf to the protoconid.

As noted previously, P^4 in *Petrogale* sometimes has a longitudinal cingulum near the base of the buccal face. This is very subdued, barely noticeable in most cases, but in a few (e.g. 77.5.631) expands posteriorly into an enamel fold or even small "pocket" which could be described as an accessory cuspule. Similarly, a subdued cingulum may be present along part of the buccal face of P_4 (e.g. 10744), or a small crest or enamel fold may extend slightly obliquely up the rear of the buccal face to fuse with the main central crest (e.g. 77.5.638). In 73.8.352 (an isolated P_4, possibly never erupted) the central portion of the main central crest of the tooth descends far below the front and rear portions, but this appears to be a malformation rather than a functional variant.

The small peg-like cuspule on the lingual face of I^1 in *Petrogale,* described in the previous section, is present in a large proportion of teeth, indeed in some samples in a majority (e.g. 37 out of 63 left and 46 out of 86 right upper first incisor teeth in the "Deepdene Cave—upper" sample). In most samples, however, a discrete peg is present only in a minority of teeth (e.g. "Deepdene Cave—lower", in 19/42 right and 15/38 left I^1), though in virtually every case there is some corresponding structure ranging from a slight swelling in the enamel to a well marked vertical buttress. In 77.11.50, this buttress culminates in a small and a larger projecting peg, and all or most of the single pegs similarly represent the culmination of buttresses.

The distribution of this peg-like cuspule appears to be random both in space and time. Thus in Devil's Lair, incisors with and without it occur in the same layer, often in the same trench, e.g. in Trench 7d, Layer Y contains 75.4.444 (with cuspule) and a specimen without cuspule stored with 77.5.532. There are teeth with these cuspules in most layers in Devil's Lair from at least as high in the sequence as Layer M (73.10.204) to as low as Layer 28 (76.9.225), almost the lowest layer containing *Petrogale.* There are numerous instances in both Deepdene Cave and Devil's Lair, though none in the small samples from the other fossil sites discussed, nor in the modern samples used for statistical comparisons. However, it does occur in modern specimen M9872 from the Warburton Range, some 1 400 km from Deepdene Cave, in what appears to be the same species as Devil's Lair and Deepdene Cave.

These morphological variants appeared to be randomly distributed both in time and space, and I was unable to identify any constant or progressive differences in tooth form.

Discussion and conclusions

Specific identity of the south-western fossil rock wallabies

Calaby (1971) suggests that the highly discontinuous distribution of rock wallaby populations has resulted in the appearance of numerous size and colour variants. Many of these have been distinguished as "species". Both Ride (1970) and Calaby (1971) recognize more than one species in northern Australia, and Kitchener and Sanson (1978) have recognized an additional species recently. But there appear to be only two species in southern Australia, *Petrogale xanthopus* and the very wide ranging and variable *P. penicillata,* taken by Ride (1970) to include *"P. lateralis"*, *"P. hacketti"* and *"P. pearsoni"*, the named south-western "species" (see Serventy 1953 for authors of and comments on the status of these taxa).

The south-western fossil samples can be interpreted as supporting the concept that discontinuous populations with distinctive characters can be regarded as conspecific. It is highly probable that the Devil's Lair sample represents a single population persisting for some 25 000 years (Balme *et al.* 1978) with only minor changes in tooth size (Table 10 and comments in the preceding section), and rather uniform tooth sizes over any given part of this time (Tables 1-6). With a lower but still high degree of probability, it may be suggested that the Deepdene Cave and "other caves" samples represent populations conspecific with that round Devil's Lair, and (at a slightly lower level of probability) with that around Yallingup Cave. Yet there are numerous statistically significant differences in tooth size (Table 7) in these samples.

Thus it would seem reasonable to give little biological weight to the statistically significant differences between south-western fossil samples and the modern Recherche Archipelago samples in some dimensions, nor between the Recherche and Quairading samples in length of P^4 (Table 7). Nor do there appear to be any constant differences in tooth form among any of these samples.

Serventy (1953) reports an opinion that Wilson Island might have a population of smaller rock wallabies than Mondrain, Combe and Salisbury Islands, in the Recherche Archipelago. Jones (1924) suggests that the Pearson Island animals (South Australia) might be smaller than those on the mainland. But if these observations are accurate for general body size, it does not seem that tooth size is necessarily closely related to body size according to the comparison of single specimens shown in Table 11.

I have not made the very extensive metrical and morphological studies of modern samples of *Petrogale penicillata* and other rock wallaby species which would be required fully to justify inclusion of the south-western fossil samples under *P. penicillata*. But for practical purposes, in the absence of any strong evidence to the contrary, I assume they can be so included.

Arrival and extinction of rock wallabies in the south-west

Except for a mislabelled modern specimen discussed by Baynes (in Baynes *et al.* 1976 p. 125), there are no rock wallaby remains in a macropod-rich deposit containing *Sthenurus*, *Zygomaturus* and numerous other extinct taxa in Mammoth Cave, with an age in excess of 37 000 yr B. P. (Merrilees 1968). But the undated deposit in Strongs Cave which contained *Petrogale* also contained *Sthenurus*, and the Labyrinth has yielded both *Petrogale* and various extinct taxa, probably in association (see notes on deposits, above).

In the lowest parts of the Devil's Lair deposit, rock wallabies are absent until about 30 000 yr. B. P., cannot be described as abundant until about 21 000 yr. B. P., are still present up to Layer D, estimated to date from about 5 000 yr. B. P., but are not certainly present in undisturbed parts of the topmost layer dated at about 300 yr. B. P. At about 19 000 yr. B. P. there was a flourishing colony near Deepdene Cave.

No rock wallabies occur in a deposit in Skull Cave, only 5 km from Deepdene Cave, over a time range covering most if not all the Holocene (Porter in press), nor are there any records of them in the Cape Leeuwin-Cape Naturaliste region in historic time (Baynes *et al.* 1976).

It would appear that rock wallabies may have arrived in the Cape Leeuwin-Cape Naturaliste region at some time prior to 30 000 yr. B. P., though they might not have built up substantial populations until nearly 20 000 yr. B. P. Balme *et al.* (1978) suggest that their time of arrival in the Devil's Lair district approximates the time of their first appearance in the deposit. But this suggestion may not be consistent with the Strongs Cave evidence (and possibly that from The Labyrinth) of contemporaneity of *Petrogale* with various large extinct taxa. At any rate, rock wallabies seem to have arrived between the unknown time of formation of the Mammoth Cave deposit and 30 000 yr. B. P., and to have disappeared from the region well before historic time and perhaps not long after the time of their last appearance in the Devil's Lair deposit, i.e. after 5 000 yr. B. P.

Implications of the rock wallaby migration and extinction

Such a record of invasion and extinction raises interesting questions: by what route, and under what kind of climate and vegetation was the invasion possible, and what changes brought about the extinction?

Since rock wallabies were not present under the vegetational and climatic *régime* of historic time, this was presumably inimical to them. For the geologically short period under discussion, it is reasonable to assume that if rocky outcrops favourable to rock wallabies once existed, they still exist, and to seek evidence of environmental changes other than in habitat.

There appears to be little doubt that one such environmental difference was vegetational. Without postulating any climatic difference, one must envisage a much greater extent of coastal plain in late Pleistocene than in late Holocene time because of glacio-eustatic effects. By postulating additionally a cooler, drier and windier climate during and for some thousands of years subsequent to the time of minimum sea level, one sees this wider coastal plain as a wider belt of heath or scrub formations than exists at present. If wind was, as it still appears to be, a major determinant of vegetational boundaries, it may be that this wider late Pleistocene coastal heath or scrub adjoined forest or other tree formations more or less along the same boundary as at present, greater wind speeds being counterbalanced by greater distance from the sea.

The likely effect of reduced effective rainfall in the late Pleistocene presumably would be reduced plant cover in any formation, but on present evidence it is difficult to estimate the extent of this reduction. Balme *et al.* (1978) present evidence from changes in the mammal fauna in Devil's Lair over a period beginning about 35 000 years ago and ending about 5 000 years ago, but point out that mammals may be less sensitive to climatic fluctuations, and their remains less reliable indices of such fluctuations, than practically any other animal group, and certainly less reliable than plant fossils. Consequently, their interpretation of the changes reflected in the Devil's Lair mammal fauna provides for a wide range of possibilities.

At one extreme, these faunal changes could be consistent with a climate only a little drier than at present, at the other extreme with a climate so much drier that profound vegetational differences from the present must be envisaged. One possibility is that about 35 000 years ago some plant formation sufficiently open to support a substantial population of *Tarsipes* was a major one near Devil's Lair, and that it remained so for several thousand years. It may have given way to woodland or forest by 20 000 years ago, but this may have been a jarrah-marri association unlike the karri high open forest of historic time. Such karri forest may have come to dominate the southern part of the Cape Leeuwin-Cape Naturaliste region only after 10 000 years ago.

The northern part of the region, including Yallingup Cave, at present is vegetationally different from the southern (Smith 1973), and it is perhaps reasonable to postulate that if Devil's Lair was surrounded at any stage by, say, jarrah-marri high woodland, Yallingup Cave would have been surrounded by jarrah-marri woodland or banksia low woodland or some other more open formation.

So far as rock wallabies are concerned, if it can be assumed that karri high open forest or jarrah-marri open forest (i.e. the main formations occupying in historic time those localities known to have harboured rock wallabies in prehistoric time) are inimical to them, then it can be assumed that other more open formations were dominant when rock wallabies invaded and flourished in the district. Wakefield (1971) suggests that a change from grassy parkland to dense tough shrubbery in western Victoria in historic time was unfavourable to *Petrogale penicillata*, lending support to the suggestion that density of plant cover is in some way influential.

If a present general characteristic of *P. penicillata* is a very wide geographical range occupied by discontinuous, widely separated populations, it is reasonable to suggest either that the species has an impressive ability to colonize and spread across unfavourable environments until it reaches favourable ones or that the present isolated populations are relics from an originally continuous one. (It would be ironic if "rock wallaby" really meant "wallaby preserved by rocks in an otherwise unsuitable environment" rather than "wallaby specialized for life among rocks" as usually understood.)

In the case of *Petrogale penicillata* migrating into the Cape Leeuwin-Cape Naturaliste region in late Pleistocene but pre-glacial-maximum time, a high degree of colonizing enterprise would appear to have been necessary. Not only would they have had very little choice of rock type, but they would have had to cross large areas completely devoid of rock outcrop of any kind.

The geology of the region is discussed by Lowry (1967), and if due allowance be made for a zone now submerged and not well known geologically, but emergent during the late Pleistocene, Lowry's map covers all the possible migratory routes to the narrow belt of dune limestone which contains all the *Petrogale* sites described above. Perhaps the most likely would be from the dissected west-facing scarp of the Darling Fault to the Whicher Range and thence to the elevated and dissected Leeuwin-Naturaliste Block. But the Whicher "Range" is a very subdued chain of low hills, quite unlike the rock wallaby habitats in Victoria illustrated by Wakefield (1963, 1971). Another more remote possibility would be along the banks of the Blackwood River if that were much more deeply entrenched than it is now, during a period of lower sea level.

The Leeuwin-Naturaliste Block is sufficiently dissected to be credible rock wallaby territory. There are collapse dolines round many caves in the central "spine" of dune limestone, occasional outcrops of gneissic basement rock, and sea cliffs in both kinds of rock. There may have been cliffs along earlier western coastlines, now submerged and blanketed by sediment. But it seems very unlikely that earlier coastlines of Geographe Bay, more or less parallel to the present coast in the vicinity of Busselton, but north of it, would have been cliffy, and hence potential migration routes for *Petrogale*.

If in addition to these geologically unfavourable conditions, the immigrant rock wallabies had to contend with unfavourable (i.e. dense) plant formations, it would seem unlikely that they would have reached the haven of the Leeuwin-Naturaliste Block. Therefore it is reasonable to suggest that plant formations were more open than at present. Of the range of possibilities allowed by the evidence of Balme *et al.* (1978), conditions close to the driest extreme may be selected as most conducive to rock wallaby migration.

With colonies once established in the Leeuwin-Naturaliste Block, no doubt there could be changes in climate and vegetation, at least in some directions, which would still permit survival. But the eventual local extinction of these rock wallaby colonies and other "non-forest mammals" could be a function of climate. Replacement of Pleistocene open plant formations by karri high open forest in the south of the region, and jarrah-marri open forest in the north and east would appear to be consistent with the rock wallaby record as well as with the known vegetational record in historic time and with the Holocene record studied by Churchill (1968).

Differences in the south-western rock wallaby samples

The analysis of the Devil's Lair fauna by Balme *et al.* (1978), on which this review of south-western rock wallabies largely depends, is itself dependent on accurate identification of fragmentary remains. These authors suggest that closer analysis, taxon by taxon, should provide some quantitative estimate of their degree of accuracy. In this instance, at least 800 specimens identified by them as *Petrogale* were re-examined by me in a specialized context later. In my opinion, less than 40 had been misidentified. It seems unlikely that this order of inaccuracy would influence their findings appreciably.

As shown in Tables 1-6, the Deepdene Cave rock wallabies had generally longer, sometimes wider and sometimes narrower cheek teeth than those around Devil's Lair, and these in turn had larger teeth than the Yallingup Cave animals. Some of these differences are statistically significant, some not (Tables 7 and 8, in which the sample with the larger mean is entered first in each pair). In the cases of significant difference the Deepdene Cave mean values show up as the largest. The "other caves" sample, drawn from the same population as that of Devil's Lair, or from populations not far to the north, does not appear to differ markedly from the Devil's Lair sample.

Thus it would appear that some factor, presumably environmental, favoured development of larger teeth in the extreme south-west corner of the prehistoric rock wallaby range. As shown above, tooth size may not be closely related to general body size, so it is difficult to suggest what these favourable environmental factors were. However, there are pointers in Table 11 to a suggestion that equable climate (in the sense of Axelrod 1976), cool summers, or some other climatic factor coupled with mainland (as against island) ranges, are involved.

Table 11 gives data on single specimens taken from the collection readily available to me and covering a large proportion of the western part of the range of *Petrogale penicillata,* mostly modern, but including prehistoric occurrences from caves north of Perth. In so far as single specimens can suggest trends, and taking Table 11 in conjunction with Tables 1-6, it would appear that island and inland specimens have smaller teeth than coastal, especially far south western, specimens.

It may be that the differences between the Deepdene Cave and Yallingup Cave populations were a regional expression of factors operating over half the continent, but much more detailed studies than mine would be needed to identify these factors.

At the one site where a long temporal succession can be examined, namely Devil's Lair, the samples are very small from layer to layer and trends correspondingly difficult to discern. From about 20 000 to 12 000 yr B. P., there may have been a slight increase in premolar size and a slight decrease in molar size in the rock wallabies. But if so, the differences were small compared with those involving different localities even in the circumscribed Cape Leeuwin-Cape Naturaliste region.

In this region, there is a chain of sites, a few kilometres apart in the north, and even more closely spaced in the south, some of which are known to have harboured rock wallabies, and many of which might have done so. This is not a geographical situation in which one would expect to find much variation in the wallabies, yet they did vary in tooth size.

I conclude that rock wallabies are sensitive to small climatic, vegetational or other differences in their immediate environment, and establish appropriate tooth sizes and perhaps other characters readily. But once established these characters remain fairly constant for long periods. Such a view is consistent with that taken by Calaby (1971) and others of the present condition of *Petrogale penicillata,* accounting for the taxonomic uncertainities surrounding this species.

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Table 1

Deciduous premolars, Petrogale

Sample	Length P^3					Posterior width P^3					Length P_3					Width P_3*				
	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V
Deepdene Cave—																				
Upper	35	4·9–5·7	5·4	0·2	4	35	2·9–3·7	3·3	0·1	3	48	4·2–4·9	4·7	0·2	4	48	2·1–2·6	2·3	0·1	6
Lower	26	5·0–5·8	5·4	0·2	4	26	2·9–3·5	3·3	0·2	5	19	4·5–4·8	4·7	0·1	2	18	2·1–2·6	2·3	0·1	6
Age Uncertain	2	5·2–5·3	5·3			2	3·2–3·5	3·4			19	4·3–4·9	4·7	0·1	3	19	2·2–2·7	2·4	0·1	4
Devil's Lair—																				
Young	2	4·8–5·1	5·0			2	2·8–3·3	3·1			3	4·4–4·9	4·6	0·3	5	4	2·3–2·4	2·4	0·1	2
Intermediate	35	4·5–5·7	5·0	0·2	4	38	2·7–3·5	3·2	0·2	7	42	4·3–5·0	4·6	0·2	4	43	1·9–2·6	2·3	0·1	6
Old	0					0					0					0				
Age Uncertain	3	4·9–5·1	5·0	0·1	3	4	3·2–3·5	3·3	0·1	4	12	4·4–5·0	4·7	0·2	4	14	2·2–2·5	2·4	0·1	4
Yallingup Cave—																				
Age Uncertain	2	4·7–4·9	4·8			2	3·1–3·2	3·2			1		4·5			1		2·1		
Other Caves—																				
Age Uncertain	3	5·0–5·5	5·3	0·2	4	3	3·1–3·5	3·3	0·2	7	2	each 4·5	4·5			2	each 2·3	2·3		
Modern—																				
Recherche	4	4·8–5·5	5·1	0·3	6	4	3·3–3·5	3·4	0·1	3	4	4·4–4·5	4·5	0·1	1	4	2·3–2·6	2·4	0·1	6
Quairading	0					0					0					0				

* Any position, usually central.

Table 2

Milk molars, Petrogale

Sample	Length dP^4					Posterior width dP^4					Length dP_4					Posterior width dP_4				
	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V
Deepdene Cave—																				
Upper	60	5·3–5·9	5·6	0·1	3	60	4·0–4·8	4·4	0·2	4	66	4·6–5·1	4·9	0·1	2	66	3·0–3·6	3·3	0·2	5
Lower	44	5·1–5·9	5·6	0·2	3	44	4·0–4·8	4·3	0·2	5	35	4·4–5·1	4·9	0·1	3	35	2·9–3·5	3·2	0·1	3
Age Uncertain	4	5·3–5·6	5·5	0·1	3	4	4·2–4·4	4·3	0·1	2	25	4·8–5·2	5·0	0·1	3	25	3·0–3·6	3·3	0·1	4
Devil's Lair—																				
Young	2	5·1–5·3	5·2			2	4·4–4·6	4·5			3	4·4–4·9	4·6	0·3	6	4	3·3–3·4	3·3	0·1	2
Intermediate	45	5·0–5·9	5·4	0·2	4	44	4·0–4·8	4·5	0·2	4	44	4·6–5·2	4·9	0·2	3	39	3·0–3·9	3·3	0·2	7
Old	3	5·1–5·5	5·2	0·2	5	3	4·0–4·4	4·2	0·2	5	0					0				
Age Uncertain	14	5·1–5·8	5·4	0·2	4	14	4·4–4·8	4·5	0·1	2	17	4·6–5·1	4·9	0·1	3	16	3·1–3·5	3·4	0·1	3
Yallingup Cave—																				
Age Uncertain	2	5·2–5·4	5·3			2	4·2–4·6	4·4			3	4·7–5·0	4·9	0·2	3	2	3·2–3·3	3·3		
Other Caves—																				
Age Uncertain	3	5·0–5·5	5·3	0·3	5	2	4·2–4·6	4·4			3	4·7–4·9	4·8	0·1	2	3	3·1–3·5	3·3	0·2	6
Modern—																				
Recherche	4	4·7–5·0	4·9	0·1	3	4	4·0–4·4	4·2	0·2	4	3	4·1–4·4	4·3	0·2	4	3	3·0–3·2	3·1	0·1	3
Quairading	0					0					0					0				

Table 3

Permanent premolars, Petrogale

Sample	Length P^4					Posterior width P^4					Length P_4					Posterior width P_4				
	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V
Deepdene Cave—																				
Upper	0					0					4	6·1–6·4	6·2	0·1	2	4	2·2–2·5	2·4	0·1	6
Lower	0					0					0					0				
Age Uncertain	0					0					2	6·4–6·7	6·6			4	2·3–2·8	2·5	0·2	8
Devil's Lair—																				
Young	4	6·5–7·1	6·7	0·3	5	4	3·5–4·1	3·8	0·3	8	3	6·2–6·4	6·3	0·1	2	4	2·2–2·7	2·4	0·2	9
Intermediate	23	6·5–7·5	7·0	0·2	3	26	3·5–4·5	4·0	0·3	7	25	5·6–6·7	6·2	0·3	4	25	2·2–2·6	2·4	0·1	6
Old	1		6·5			1		2·8			1		6·0			0				
Age Uncertain	6	6·9–7·4	7·2	0·2	3	5	3·9–4·7	4·3	0·4	8	7	5·9–6·4	6·2	0·2	3	6	2·2–2·5	2·3	0·1	4
Yallingup Cave—																				
Age Uncertain	4	6·4–7·0	6·6	0·3	4	4	3·7–3·9	3·8	0·1	3	4	5·8–6·1	6·0	0·2	2	3	2·0–2·3	2·1	0·2	8
Other Caves—																				
Age Uncertain	4	6·6–7·1	6·9	0·2	3	4	3·7–4·2	4·0	0·2	6	3	6·0–6·3	6·2	0·2	3	3	2·0–2·5	2·3	0·3	12
Modern—																				
Recherche	6	6·2–7·3	6·8	0·5	7	8	3·0–3·7	3·3	0·3	8	8	5·4–6·3	6·0	0·4	6	8	1·9–2·7	2·3	0·3	13
Quairading	3	6·1–6·5	6·3	0·2	3	3	3·2–3·4	3·3	0·1	4	1		5·2			1		2·0		

Table 4

First molars, Petrogale

Sample	Length M^1 N	Length M^1 O.R. mm	Length M^1 $\overline{X}$ mm	Length M^1 s mm	Length M^1 V	Anterior width M^1 N	Anterior width M^1 O.R. mm	Anterior width M^1 $\overline{X}$ mm	Anterior width M^1 s mm	Anterior width M^1 V	Length M_1 N	Length M_1 O.R. mm	Length M_1 $\overline{X}$ mm	Length M_1 s mm	Length M_1 V	Anterior width M_1 N	Anterior width M_1 O.R. mm	Anterior width M_1 $\overline{X}$ mm	Anterior width M_1 s mm	Anterior width M_1 V
Deepdene Cave—																				
Upper	3	5·7–6·0	5·6	0·2	3	1		4·6			7	5·5–5·8	5·7	0·1	2	1		3·8		
Lower	8	5·8–6·0	5·9	0·1	1	3	4·6–4·9	4·8	0·2	3	6	5·5–5·9	5·8	0·1	2	5	3·3–3·5	3·7	0·1	2
Age Uncertain	5	5·8–6·0	5·9	0·1	2	3	4·9–5·1	5·0	0·1	2	22	5·4–6·1	5·8	0·1	2	11	3·3–3·9	3·6	0·2	5
Devil's Lair—																				
Young	5	5·3–5·8	5·6	0·2	4	3	4·7–5·0	4·8	0·2	3	4	5·4–5·7	5·5	0·1	2	4	3·3–3·7	3·5	0·2	7
Intermediate	27	5·3–6·2	5·7	0·3	5	25	4·7–5·4	5·0	0·2	4	33	4·8–6·0	5·5	0·3	6	28	3·1–3·9	3·5	0·2	6
Old	0					0					0					0				
Age Uncertain	12	5·6–6·3	5·8	0·2	3	14	4·6–5·4	5·1	0·5	9	20	4·9–5·8	5·5	0·2	4	20	3·3–3·7	3·5	0·1	3
Yallingup Cave—																				
Age Uncertain	2	5·6–5·7	5·7			2	5·0–5·2	5·1			4	5·2–5·5	5·4	0·1	3	4	3·3–3·6	3·5	0·1	4
Other Caves—																				
Age Uncertain	4	5·5–6·0	5·7	0·2	4	4	4·7–5·2	5·0	0·2	4	3	5·4–5·5	5·5	0·1	1	3	3·5–3·6	3·5	0·1	2
Modern—																				
Recherche	7	5·0–5·8	5·4	0·3	5	7	4·4–4·9	4·6	0·2	4	4	5·0–5·3	5·1	0·1	3	4	3·0–3·7	3·3	0·3	9
Quairading	2	5·3–5·6	5·5			1		4·7			0					1		3·5		

Table 5

Second and third molars, Petrogale

Sample	Length M²					Anterior width M²					Length M₂					Anterior width M₂				
	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V
Deepdene Cave	2	each 6·9	6·9			2	5·4–5·6	5·5			9	6·2–6·6	6·4	0·1	2	8	3·9–4·4	4·1	0·2	5
Devil's Lair	24	5·6–7·0	6·4	0·3	1	20	5·2–6·1	5·7	0·3	5	35	6·0–6·8	6·4	0·2	4	32	3·8–4·5	4·2	0·2	4
Yallingup Cave	2	6·5–6·6	6·6			2	5·3–5·5	5·4			4	5·9–6·2	6·1	0·1	2	4	3·9–4·3	4·0	0·2	5
Other Caves	3	6·4–6·8	6·6	0·2	3	4	5·2–5·7	5·4	0·2	4	2	6·1–6·3	6·2			2	4·1–4·2	4·2		
Modern—																				
Recherche	9	5·8–6·5	6·2	0·2	2	9	4·9–5·4	5·1	0·2	3	11	5·2–5·9	5·5	0·3	5	11	3·4–4·0	3·8	0·2	5
Quairading	3	5·9–6·2	6·1	0·2	3	2	each 5·0	5·0			1		5·5			1		3·8		

Sample	Length M³					Anterior width M³					Length M₃					Anterior width M₃				
	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V
Deepdene Cave	2	7·1–7·6	7·4			2	5·9–6·0	6·0			10	6·4–7·6	7·0	0·4	5	10	4·3–4·8	4·6	0·2	4
Devil's Lair	17	6·2–7·4	7·0	0·4	5	16	5·6–6·4	6·2	0·2	4	24	6·5–7·4	7·0	0·2	3	17	4·4–5·2	4·6	0·2	5
Yallingup Cave	1		7·4			1		6·0			2	6·5–7·1	6·8			1		4·7		
Other Caves	1		7·2			2	each 5·9	5·9			2	6·5–6·9	6·7			2	4·3–4·4	4·4		
Modern—																				
Recherche	8	5·9–7·1	6·6	0·5	7	9	5·0–5·9	5·6	0·3	5	11	6·2–7·2	6·7	0·3	5	10	4·0–4·6	4·3	0·2	4
Quairading	2	6·6–7·2	6·9			2	5·5–5·8	5·7			1		6·1			1		4·0		

Table 6

Fourth molars, Petrogale

Sample	Length M^4					Anterior width M^4					Posterior width M^4				
	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V
Deepdene Cave	1		7·5			1		5·9			1		5·3		
Devil's Lair	14	6·7–7·8	7·4	0·3	4	10	5·8–6·9	6·3	0·3	5	13	5·0–5·7	5·4	0·2	4
Yallingup Cave	2	7·6–7·7	7·7			1		6·0			1		5·2		
Other Caves	0					0					0				
Modern—															
Recherche	7	6·5–7·5	7·0	0·4	5	7	5·2–5·8	5·7	0·2	4	7	4·7–5·4	5·0	0·3	5
Quairading	1		7·4			1		5·9			1		5·4		

Sample	Length M_4					Anterior width M_4					Posterior width M_4				
	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V	N	O.R. mm	$\overline{X}$ mm	s mm	V
Deepdene Cave	9	6·8–7·9	7·4	0·4	6	7	4·5–5·0	4·8	0·3	5	8	4·2–4·7	4·4	0·2	3
Devil's Lair	14	6·8–7·7	7·3	0·3	4	13	4·5–5·2	4·9	0·5	10	14	4·3–4·7	4·5	0·1	3
Yallingup Cave	1		7·2			1		4·9			1		4·3		
Other Caves	0					0					0				
Modern—															
Recherche	8	6·4–7·6	6·8	0·4	6	8	4·3–4·8	4·6	0·2	4	6	3·7–4·3	4·2	0·3	7
Quairading	2	6·4–7·0	6·7			1		4·4			1		4·3		

Table 7

Some differences between pairs of Petrogale *samples, significant at 5% level on 2-sided Student's-t test*

Dimension	Samples compared	t	Degrees of freedom
Length, P^3	Deepdene Cave, upper/modern, Recherche	2·45	37
Length, P^3	Deepdene Cave, lower/Devil's Lair, intermediate	7·00	59
Posterior width, P^3	Deepdene Cave, lower/Devil's Lair, intermediate	9·75	62
Length, P_3	Deepdene Cave, upper/Devil's Lair, intermediate	2·25	98
Length, dP^4	Deepdene Cave, lower/Devil's Lair, intermediate	4·70	87
Length, dP^4	Deepdene Cave, upper/modern, Recherche	9·71	62
Posterior width, dP^4	Deepdene Cave, upper/Deepdene Cave, lower	2·94	102
Posterior width, dP^4	Devil's Lair, intermediate/Devil's Lair, old	2·27	45
Length, dP_4	Devil's Lair, intermediate/Devil's Lair, young	3·00	45
Posterior width, dP_4	Devil's Lair, young/modern, Recherche	2·60	5
Length, P^4	Devil's Lair, intermediate/Devil's Lair, young	2·33	25
Length, P^4	Modern—Recherche/Quairading	3·66	7
Posterior width, P_4	Deepdene Cave, upper/Yallingup Cave	2·79	5
Posterior width, P_4	Devil's Lair, intermediate/Yallingup Cave	3·50	26
Length, M^1	Deepdene Cave, lower/Deepdene Cave, upper	4·40	9
Length, M^1	Deepdene Cave, lower/Devil's Lair, intermediate	2·08	33
Length, M^1	Deepdene Cave, lower/modern, Recherche	5·71	13
Length, M_1	Deepdene Cave, lower/Devil's Lair, intermediate	2·27	37
Length, M_1	Deepdene Cave, lower/Yallingup Cave	4·43	8
Length, M_1	Yallingup Cave/modern, Recherche	3·00	6
Anterior width, M_1	Deepdene Cave, lower/Devil's Lair, intermediate	2·05	31
Anterior width, M^2	Devil's Lair, all together/modern, Recherche	4·17	27
Length, M^3	Devil's Lair, all together/modern, Recherche	2·33	23
Length, M_2	Deepdene Cave, all together/Yallingup Cave	3·57	11
Length, M_2	Devil's Lair, all together/Yallingup Cave	2·38	37
Anterior width, M_2	Devil's Lair, all together/Yallingup Cave	2·24	34
Anterior width, M_3	Deepdene Cave, all together/modern, Recherche	3·94	18
Devil's Lair—Anterior width, M^4/Posterior width, M^4		8·92	21
Deepdene Cave—Anterior width, M_4/Posterior width, M_4		3·85	13

Table 8

Some differences between pairs of Petrogale *samples, not significant at 5% level on 2-sided Student's-t test*

Dimension	Samples compared	t	Degrees of freedom
Length, P^4	Devil's Lair, young/Yallingup Cave	0·54	6
Posterior width, P^4	Devil's Lair, intermediate/Devil's Lair, young	1·32	28
Posterior width, P^4	Devil's Lair, intermediate/Yallingup Cave	1·42	28
Length, P_4	Deepdene Cave, upper/Yallingup Cave	2·00	6
Length, M^1	Devil's Lair, intermediate/Devil's Lair, young	0·81	30
Length, M_1	Deepdene Cave, lower/Deepdene Cave, upper	1·80	11
Length, M^2	Modern—Recherche/Quairading	0·71	10
Anterior width, M_2	Devil's Lair, all together/Deepdene Cave, all together	1·47	38
Length, M_4	Deepdene Cave, all together/Devil's Lair, all together	0·66	21

Table 9

Comparison of tooth dimensions (mm) in specimens of macropodid species often found with Petrogale *with mean dimensions of south western fossil* Petrogale

Catalogue No.	P^3 1 x p.w.	dP^4 1 x p.w.	P^4 1 x p.w.	M^1 1 x a.w.	M^2 1 x a.w.	M^3 1 x a.w.	M^4 1 x a.w. x p.w.
Petrogale—							
(mean)	5·2 x 3·3	5·5 x 4·4	6·8 x 4·0	5·8 x 5·0	6·5 x 5·6	7·1 x 6·2	7·5 x 6·3 x 5·4
Macropus irma—							
77.6.496	5·7 x 3·8	6·4 x 5·2		6·5 x 5·7	7·2 x 6·3	7·7 x 6·1	
M6788			6·3 x 3·8	6·7 x 5·8	7·3 x 6·4	8·1 x 6·6	8·5 x 6·0 x 5·5
Macropus eugenii—							
65.10.115a	— x 2·6	4·3 x 3·7	4·7 x 2·5	5·0 x 4·3	5·4 x 4·5	(P^4 extracted)	
69.3.781			4·3 x 2·8	5·5 x 4·9	5·7 x 5·1	6·2 x 5·4	6·8 x 5·5 x 4·6
69.3.776	4·8 x 3·0	4·8 x —		5·2 x 4·3	5·7 x 5·2	6·7 x 5·4	
Setonix brachyurus—							
77.6.323			7·2 x 3·5	4·2 x 4·2	4·7 x 4·5	5·1 x 4·8	5·1 x 4·4 x 3·5
77.3.449	4·9 x 3·5	4·1 x 4·0		4·4 x 4·1			

Catalogue No.	P_3 1 x w.	dP_4 1 x p.w.	P_4 1 x p.w.	M_1 1 x a.w.	M_2 1 x a.w.	M_3 1 x a.w.	M_4 1 x a.w. x p.w.
Petrogale—							
(mean)	4·7 x 2·3	4·9 x 3·3	6·2 x 2·4	5·6 x 3·5	6·3 x 4·2	7·0 x 4·6	7·3 x 4·9 x 4·4
Macropus irma—							
70.12.458	4·9 x 3·2	6·1 x 4·4		6·7 x 4·6	7·2 x 5·1	7·8 x 5·8	
M6788			4·5 x 2·6	6·3 x 4·7	6·9 x —	7·6 x 5·5	7·4 x 5·5 x 5·0
66.2.114			4·7 x 2·5	6·0 x —	7·4 x —	7·7 x 5·5	6·9 x 5·2 x 4·8
Macropus eugenii—							
73.10.1354			3·8 x 1·9	4·7 x 3·2	4·7 x 3·5	5·4 x 4·1	5·6 x 4·1 x 3·9
65.10.115	3·7 x 1·8	4·5 x 2·8	3·5 x 1·5	4·7 x 3·1	5·0 x 3·5	(P_4 extracted)	
Setonix brachyurus—							
10754			6·1 x 3·0	4·6 x —	4·8 x 3·8	5·1 x 4·2	5·4 x 4·2 x 4·1
73.7.571	4·5 x 2·4*	3·6 x 2·8					
70.12.80		3·9 x 2·7		4·3 x 3·1			

* Maximum width of P_3 is anterior.

Table 10

Measurements (mm) of anterior cheek teeth of Petrogale *from various layers in Devil's Lair excavations of* 1973–76. *Left side only. Teeth on same horizontal line not necessarily associated.*

Layer	C^{14} Date (Yr. B.P.)	P^3 1 x p.w.	dP^4 1 x p.w.	P^4 1 x p.w.	M^1 1 x a.w.	P_3 1 x w	dP_4 1 x p.w.	P_4 1 x p.w.	M_1 1 x a.w.
D				7·1 x 4·1					
	6 490 ± 145								
H					5·8 x —				
	12 050 ± 140								
Hearth 2								6·4 x 2·5	
M	11 960 ± 140		5·0 x 4·5	6·9 x 3·8	5·5 x 4·9	4·9 x 2·2		5·9 x 2·6	
Hearth y						4·3 x 2·3			
Sub MM							4·7 x 3·2		5·9 x 3·5
N		5·0 x 3·2							
O		— x 2·7	5·5 x 4·7	7·2 x 4·0	5·7 x 5·0	4·8 x 2·3	4·8 x —	6·3 x 2·5	5·5 x 3·7
			5·5 x 4·5	7·2 x 4·0	5·4 x 5·0	4·7 x 2·3	5·0 x 3·8	6·2 x 2·3	5·5 x 3·5
			5·2 x 4·1	6·9 x 4·3	5·3 x 4·7	4·9 x 2·6		5·8 x 2·2	5·8 x 3·8
			5·4 x 4·4	7·4 x 4·5		4·8 x 2·4		6·3 x 2·6	5·5 x 3·7
						4·9 x 2·5			5·0 x 3·6
						4·7 x 2·2			
						4·7 x 2·1			
P			5·6 x 4·8						
			5·3 x —						
Q		5·1 x 3·0	5·1 x 4·6		5·7 x 4·7		5·0 x 3·4	5·6 x 2·4	
		5·0 x 3·0					4·8 x 3·5		
		5·0 x 3·2					4·6 x 3·0		
		5·0 x 3·0							
T + U								6·6 x 2·5	
U			5·6 x 4·7			4·6 x 2·3	4·8 x 3·3		5·5 x 3·3
U + V						4·7 x 2·3	5·0 x —		
V				7·2 x 4·5		5·0 x 2·4	5·2 x 3·6		5·9 x 3·7
						4·7 x 2·2	5·2 x 3·2		
							5·0 x 3·0		

Table 10—*continued.*

Layer	C^{14} Date (Yr. B.P.)	P^3	dPI	PI	MI	PI	dPI	PI	MI
		1 x p.w.	1 x p.w.	1 x p.w.	1 x a.w.	1 x w	1 x p.w.	1 x p.w.	1 x a.w.
W		—x 3·3	5·7 x 4·6		5·9 x 5·0				
W + X				—x 3·7					
X		5·2 x 3·4					4·8 x 3·1		
Y			5·6 x 4·5	—x 3·8	6·1 x —	4·7 x 2·2			
Z		5·1 x 3·1				4·5 x 2·4	4·9 x 3·4		
						4·4 x 2·2	4·6 x 3·1		
2			5·7 x 4·5		5·8 x 5·0			6·5 x 2·6	
3		5·0 x 3·5	5·5 x 4·7		5·8 x 5·4				
3 + 4					5·4 x 4·9	4·5 x 2·5			
4		5·1 x 3·2		6·9 x 3·9			5·2 x 3·5	6·0 x 2·5	
		4·9 x 2·9							
5		4·9 x 3·4	5·4 x 4·4		5·7 x 4·7				
		4·7 x 3·3							
6		4·8 x 3·1	5·1 x 4·4	6·9 x 4·0	5·4 x 5·3	4·6 x 2·4	5·0 x 3·5	5·9 x 2·2	5·5 x —
		4·7 x 2·9				—x 2·5	4·8 x 3·1		5·7 x 3·2
		4·9 x 3·2				4·3 x 1·9			5·7 x 3·2
		4·5 x 2·8							
7	19 000 ± 250		—x 4·5				4·8 x 3·1		
9	19 250 ± 900								
10	20 400 ± 1 000								
10 d + e			5·5 x 4·4						
			5·1 x 4·3						
11			5·1 x 4·0						
24				6·5 x 2·8*				6·0 x —	
28	24 600 ± 1 500								
	27 700 ± 700								

* A worn, rather corroded, isolated tooth.

Table 11

Tooth dimensions (mm) in some individual Petrogale *specimens, probably conspecific, from localities remote from one another*

Specimen No.	P^3 1 x p.w.	dP^4 1 x p.w.	P^4 1 x p.w.	M^1 1 x a.w.	M^2 1 x a.w.	M^3 1 x a.w.	M^4 1 x a.w. x p.w.
9908—Pearson Island—male			6·3 x 3·5	worn	6·0 x 5·3	6·9 x 5·8	unerupted
M4428—Combe Island—female			6·2 x 3·3	worn	6·0 x 5·0	6·3 x 5·3	7·0 x 5·7 x 4·8
M4424—Wilson Island—female			6·3 x 3·1	5·0 x 4·6	6·0 x 5·2	7·0 x 5·7	7·5 x 5·8 x 5·0
65.10.62—Deepdene Cave	5·2 x 3·5	5·4 x 4·4		5·8 x 4·9			
63.8.15—Yallingup Cave			7·0 x 3·8	5·7 x 5·2	6·5 x 5·5	7·4 x 6·0	7·6 x 6·0 x 5·2
65.10.169—Dunstan's Quarry, Wanneroo district	5·4 x 3·3	5·6 x 4·6		5·9 x 4·7			
M4308*—North Kellerberrin	4·9 x 2·9	4·9 x 4·2	6·4 x 3·0	5·8 x 4·8	6·3 x 5·2		
M14989—Fortescue River	5·5 x 3·5	4·8 x 3·9		5·5 x 4·6			
M9872—Warburton Range	5·0 x 3·0	5·2 x c3·9					

Specimen No.	P_3 1 x w.	dP_4 1 x p.w.	P_4 1 x p.w.	M_1 1 x a.w.	M_2 1 x a.w.	M_3 1 x a.w.	M_4 1 x a.w. x p.w.
9908—Pearson Island—male			6·0 x 2·2	worn	5·9 x 3·9	6·6 x 4·6	not completely erupted
M4428—Combe Island—female			5·5 x 2·1	worn	5·6 x 4·0	6·6 x 4·3	6·4 x 4·6 x 4·2
M4424—Wilson Island—female			worn	worn	5·4 x 3·7	6·5 x 4·3	6·7 x 4·8 x 3·7
77.11.49a—Deepdene Cave			6·4 x 2·3	5·8 x 3·9	6·6 x 4·4	7·5 x 4·7	7·8 x 5·0 x 4·3
76.2.99—Yallingup Cave			6·1 x 2·1	5·2 x 3·5	6·2 x 4·3	7·1 x 4·7	7·2 x 4·9 x 4·3
71.11.93—Orchestra Shell Cave, Wanneroo district			6·3 x 2·5	5·5 x 3·6	6·2 x 4·2	6·6 x 4·6	unerupted
M4308*—North Kellerberrin	4·2 x 2·1	4·6 x 3·2	5·7 x 1·8	4·8 x 3·2	6·0 x 3·9		
M14989—Fortescue River	4·6 x 2·3	4·6 x 3·2		5·4 x 3·5			
M9872—Warburton Range	4·3 x 2·2	4·7 x c2·9					

* P^4_4 erupted one side, P^3_3 remaining on other.

Appendix 1

Canis and Thylacinus in Yallingup Cave

Perhaps the most significant specimen at the "thylacine locality" in Yallingup Cave was a maxillary fragment (63.6.26) from a dog, presumably a dingo, in the uppermost 7½ cm spit immediately underlying "1st dripstone". Whatever the period of time represented by "1st dripstone", which might be considerable, there is an inference that dogs arrived in the district before thylacines became extinct there. There is no reason to doubt the accuracy of the record, because the dog specimen has a chalky appearance like other specimens from below the dripstones, whereas the thylacine specimens from above "1st dripstone" have a more robust and fresher appearance. The occurrence is consistent with the suggestion made by Archer (1975) and others that there is a causal connection between the arrival of dogs and the extinction of thylacines in a region.

Among other taxa from the same "spit" as the dog were *Macropus fuliginosus* (63.6.27), murids (including *Notomys*, 77.8.54) and an unidentified snake, but neither in this "spit" nor the ones successively beneath, but above "2nd dripstone", was *Petrogale* represented.

Appendix 2

Lagorchestes in the south-west

During the examination of several hundred lower milk molars of *Petrogale,* not only those represented in Table 2, but also those from the opposite sides (not measured) watch was kept for any variant which might resemble specimen 70.12.1132 from Devil's Lair (see Dortch and Merrilees 1972, p. 111; Baynes *et al.* 1976, p. 108). At the time of writing, this is still the only specimen from Devil's Lair giving any reliable basis for recording *Lagorchestes* from the prehistoric fauna, though several other small fragments have been diagnosed tentatively as *Lagorchestes*. The suspicion naturally arises that 70.12.1132 is an aberrant *Petrogale* specimen.

It consists of the anterior portion of a right dentary of a very young animal, with a broken incisor stump, P_3 erupted but virtually unworn, dP_4 perhaps not fully erupted and M_1 erupting. This dentary fragment has been subjected to slight polishing, common in Devil's Lair material, by post-mortem processes not yet understood but rendering difficult a decision on the extent of wear during the animal's life. There is slight damage, almost certainly post-mortem, to dP_4 and M_1. The permanent premolar has been extracted from its crypt, but consists only of a partially formed enamel cap, too immature to be a good guide to the finished size and shape.

Measurements of the cheek teeth in 70.12.1132, made in the same way as for the *Petrogale* samples reported in Tables 1-11 are as follows: P_3 = 3.6 x 1.8 mm, dP_4 = 4.5 x 3.1 mm, M_1 = 4.8 x 3.2 mm, P_4 (extrapolated) = c. 3.9 x c. 1.3 mm. The equivalent dimensions in modern *Lagorchestes hirsutus* (M1572, from the Warburton Range region) are: P_3 = 3.1 x 1.4 mm, dP_4 = 4.0 x 2.8 mm, M_1 = 4.5 x 3.1 mm, and P_4 in M7965 from Bernier Island = 4.0 x 1.5 mm.

Thus both lengths and widths of P_3 and P_4 in 70.12.1132 fall completely outside the observed range of the Devil's Lair *Petrogale* sample, or the other fossil or modern samples reported in Tables 1 and 3, while the lengths and widths of dP_4 and M_1, while just falling within the observed ranges, are much less than the means in *Petrogale.*

On metrical grounds alone, 70.12.1132 can be rejected as a *Petrogale* variant, and this is supported by the absence of any dP_4 in the large *Petrogale* sample which resembles that in 70.12.1132. The forelink in dP_4 in 70.12.1132 is very prominent and crosses the anterior shelf obliquely in a way characteristic of *Lagorchestes.* Further, P_3 in 70.12.1132 has a concavity in the lingual face which does not appear as a variant in *Petrogale* whereas it is characteristic of *Lagorchestes*. However, there are resemblances in shape between P_3 and M_1 in 70.12.1132 and in undoubted *Petrogale,* though the forelink in M_1, is somewhat thicker and more sinuous than is modal for *Petrogale.*

Tooth dimensions in 70.12.1132 are greater than in the modern specimens quoted above, and Dortch and Merrilees (1972) therefore ascribed the specimen to *Lagorchestes leporides* rather than to *L. hirsutus,* which is more likely on biogeographical grounds. In conjunction with the discussion above of size variants in *Petrogale,* the size differences in *Lagorchestes* perhaps may be regarded as of little significance.

I conclude that 70.12.1132 does indeed represent *Lagorchestes, probably L. hirsutus.*